5

Vegetational consequences of the angiosperm diversification

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Palynological and megafossil evidence from many geographical areas indicates that the angiosperms first attained ecological importance during the mid-Cretaceous (Brenner, 1963; Doyle & Hickey, 1976; Hughes, 1976) and that this led to profound changes in terrestrial plant communities. This chapter briefly examines the transition from gymnosperm-dominated to angiosperm-dominated vegetation. First, it reviews a sequence of Early Cretaceous to Paleocene fossil floras, concentrating on megafossil data from middle palaeolatitudes in the Northern Hemisphere, and then discusses the major changes that occurred in the composition and structure of terrestrial vegetation between the earliest Cretaceous and the Paleocene. Particular attention is directed toward changes in the relative proportions of five major groups of plants: pteridophytes, cycadophytes, conifers, angiosperms and 'other' seed plants (e.g. *Czekanowskia*, *Ginkgo*).

Review of floras

Neocomian floras

During the Neocomian, as in the Middle and Late Jurassic, latitudinal climatic gradients and floristic provinces were much less marked than they are today, as a result of less dispersed land masses and a more equable global climate (Parrish, this volume, Chapter 3). In the Northern Hemisphere most authors recognize a northern, Siberian–Canadian, floristic province and a southern, Euro-Sinian (Indo-European) province (Figure 5.1(*a*), e.g. Vakhrameev, 1964; Batten, 1984; Vakhrameev *et al.*, 1978). The classic Middle Jurassic flora from Yorkshire (Harris, 1961*a*, 1964, 1969, 1979; Harris, Millington & Miller, 1974) has an abundance

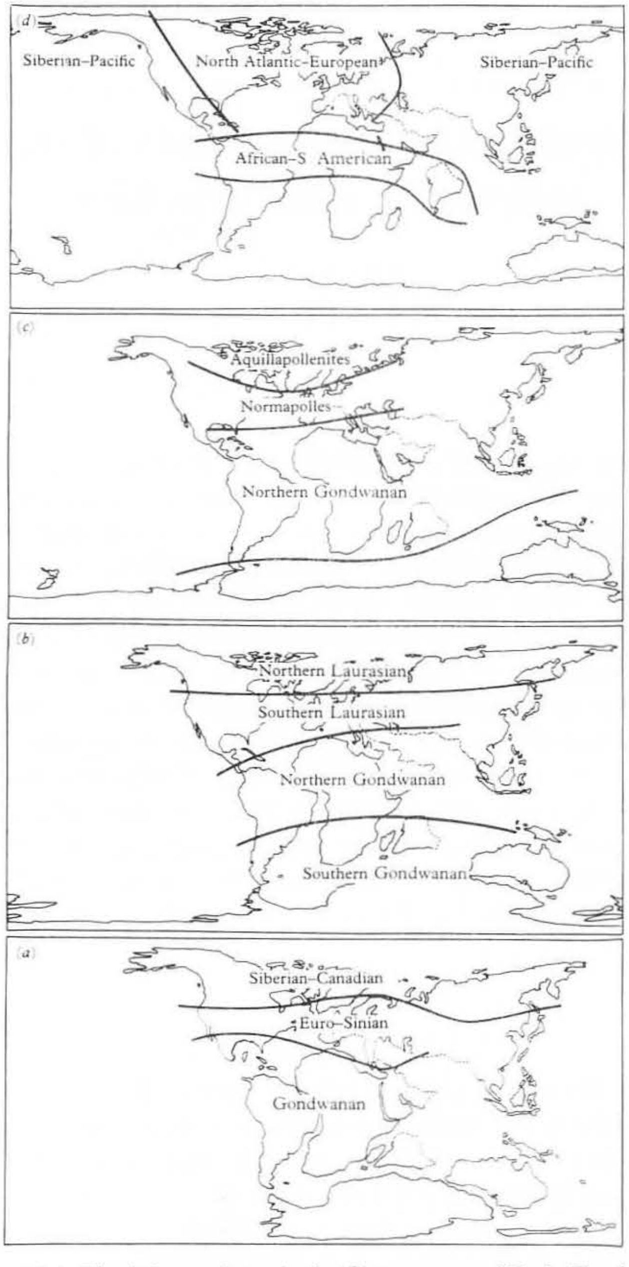

Figure 5.1. Floristic provinces in the Cretaceous and Early Tertiary. (*a*) Neocomian (based on Vakhrameev *et al.*, 1978; Batten, 1984). (*b*) Cenomanian (based on Brenner, 1976; Batten, 1984). (*c*) Santonian–Campanian (based on Batten, 1984). (*d*) Paleocene (based on Krutzsch, 1967). (All base maps redrawn from Smith *et al.*, 1981.)

of cycadophytes and is typical of the Euro-Sinian province, while Siberian–Canadian floras exhibit lower generic and specific diversity, less abundant cycadophytes, a higher proportion of Czekanowskiales, Ginkgoales, and conifers, and relatively few endemic taxa (Batten, 1984).

Pteridophytes typically account for 30% of the species in Jurassic and Neocomian floras (Figure 5.2(*a*)). Ferns were particularly abundant and diverse, and most were representatives of the extant families Dicksoniaceae, Dipteridaceae, Gleicheniaceae, Marattiaceae, Matoniaceae, Osmundaceae and Schizaeaceae. *Tempskya* (a tree fern of unknown systematic position; Ash & Read, 1976) and *Weichselia* (a xeromorphic plant, probably related to extant Matoniaceae; Alvin, 1968; Daber, 1968) are two of the most characteristic Early Cretaceous ferns. In forested situations, ferns probably dominated the ground cover, but a few may also have been epiphytes (e.g. *Todites princeps*, Osmundaceae; Harris, 1961*a*). Abundant megaspores of probable heterosporous water ferns (e.g. *Arcellites*; Batten, 1974) indicate that these plants were probably important colonizers of open water, and ferns also formed extensive stands in unwooded areas that would today be dominated by angiosperm herbs (Apert, 1973; Harris, 1981). Probable gleicheniaceous and schizaeaceous spores are especially abundant in Neocomian palynofloras, and many extant species in these families are characteristically plants of open habitats (R. G. Stolze, personal communication). In the Weald Clay of southern England the abundance of fusainized matoniaceous and gleicheniaceous leaves at some localities, combined with an almost complete absence of gymnosperm fossils, suggests a fern-savanna from which conifers and other gymnosperms were perhaps excluded by periodic fires (Harris, 1981).

Although lycopods and sphenopsids were less diverse than ferns in the Early Cretaceous, they were locally important in the herbaceous flora. The abundance of *Isoetes*-like and *Selaginella*-like megaspores (e.g. Kovach & Dilcher, 1985) and lycopod and sphenopsid megafossils (e.g. *Nathorstiana*; Mägdefrau, 1932; and *Equisetum*; Watson, 1983) suggests that lycopods and sphenopsids frequently dominated partially flooded areas and perhaps other open habitats.

Cycadophytes typically account for about 30% of the species in Jurassic and Neocomian megafloras (Figure 5.2(*a*)) and include at least three different kinds of plants with pinnate leaves: true cycads, Bennettitales (Cycadeoidales) and a heterogeneous group of seed ferns with pinnate foliage that is difficult to separate from that of true cycads. Few Mesozoic cycads are known in detail, but the data available (Harris, 1961*b*) suggest a reproductive biology similar to that of extant species. The seeds of *Beania* are among the largest known for Jurassic and early Cretaceous gymnosperms and, as in extant cycads, these seeds contain a thick megaspore membrane that probably correlates with a well-developed megagametophyte. At least some Mesozoic cycads were pachycaul (e.g. Smoot, Taylor & Delevoryas, 1985) but others were probably slender, highly branched (Harris, 1961*b*; Kimura & Sekido, 1975) and had significantly smaller leaves than do their extant relatives.

Despite the similarities between the leaves of the Bennettitales and Mesozoic cycads, the two groups differed substantially in most other features (Harris, 1976), and although few of these plants are well understood it is clear that extant cycads are a misleading guide to the biology and ecology of the Bennettitales (Crane, 1985). Studies of dispersed cuticles show that the Bennettitales were abundant in Neocomian vegetation (e.g. Oldham, 1976). In addition to pachycaul forms, such as *Cycadeoidea* (e.g. Crepet, 1974) and *Monanthesia* (Delevoryas, 1959), at least two other kinds of growth habit occur within the Bennettitales. The stems of *Zamites gigas* (Harris, 1969) and similar plants (e.g. *Ischnophyton*, Delevoryas & Hope, 1976) were probably sparsely branched, with a tuft of leaves and persistent leaf bases at the apex as in some palms. In contrast, the stems of *Wielandiella* (Nathorst, 1902; Harris, 1932) and *Ptilophyllum* plants were slender, frequently sympodially branched and bore leaves that abscissed cleanly from the stem (Harris, 1969, 1973). Even these slender bennettitalean stems were relatively thick in relation to the size of leaves that they bore, and among Recent angiosperm trees this is characteristic of plants that are ecologically intolerant of shade (White, 1983). Most bennettitalean leaves consist of an elongated main rachis bearing a segmented pinnately arranged lamina and thus conform to morphologies that are theoretically more advantageous for early successional rather than climax forest trees (Givnish, 1971). On average, bennettitalean leaves are an order of magnitude smaller than those of extant cycads (microphylls or small mesophylls) and even in otherwise mesomorphic vegetation they often exhibit marked xeromorphic tendencies, such as reflexed pinnae, well developed hairs or papillae on the abaxial surface, and sunken or occluded stomata (e.g. Harris, 1969). In their reproductive biology, most Bennettitales were probably insect pollinated (Crepet & Friis, this volume, Chapter 7) and the seeds were either dispersed by animals or perhaps released by fire (Harris, 1973). Small seed size is consistent with the idea that the Bennettitales colonized open habitats (Harris, 1973;

Harper, Lovell & Moore, 1970). Silicified seeds contain well-preserved dicotyledonous embryos (Wieland, 1906), but few gametophytes (Sharma, 1974). Combined with the lack of a thick maceration-resistant megaspore membrane (Harris, 1954) and the precocious differentiation of the integument (Crepet & Delevoryas, 1972) this may suggest that bennettitalean ovules, like those of angiosperms and Gnetales, were progenetic (Doyle, 1978) and passed rapidly through pollination, gametophyte development, fertilization and embryogenesis. Taken together, these features of reproductive biology, combined with stem and leaf morphology, support the suggestion that cycadophytes were the predominant shrubs of Mesozoic vegetation (Krassilov, 1981).

Current knowledge of the third group of cycadophytes, the pinnate-leaved seed ferns (e.g. *Ctenozamites*) is extremely poor. This group probably includes taxa of widely different relationships, and useful generalizations concerning their probable ecology and biology are not yet possible.

Conifers typically account for about 20% of the species in Neocomian and Jurassic megafloras (Figure 5.2(*a*)). The extant conifer families Araucariaceae, Cupressaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, and Taxaceae appear in the fossil record either during the Triassic or Jurassic and all are recorded from the Northern Hemisphere (Miller, 1982; Zhou, 1983). Several extinct conifer genera cannot be assigned reliably to extant families (Harris, 1976), while others are included in the extinct families Cheirolepidiaceae (also known as Hirmerellaceae, producers of *Classopollis* pollen) and Podozamitaceae (interpreted as cycadophytes in many older treatments of Mesozoic floras). The Cheirolepidiaceae were particularly important in Late Jurassic and Early Cretaceous vegetation and may have occupied a variety of habitats, particularly those that were dry or had saline groundwater (Alvin, 1983; Upchurch & Doyle, 1981).

The remaining category of 'other' seed plants includes taxa such as *Baiera*, *Czekanowskia*, Gnetales, *Ginkgo* and *Solenites* that together typically account for 10% to 15% of Neocomian and Jurassic megafloras (Figure 5.2(*a*)). At least some Jurassic and Early Cretaceous *Ginkgo* seems to have been similar to extant *G. biloba*, although the seeds and pollen cones were smaller (Harris *et al.*, 1974). The Caytoniales were slender, branched, plants (Harris, 1971), with leaves that appear to be palmately compound, although the leaflets are attached apically in two pairs. *Caytonia* seeds were small and perhaps dispersed by animals, with the fleshy 'cupule' acting as the 'reward' for the dispersal vector.

Caytonia seeds have seed cuticles similar to those of the Bennettitales (Harris, 1954) and may also have been progenetic in their gametophyte and embryo development. The structure and biology of the Czekanowskiales is poorly understood. Their most distinctive vegetative feature is the presence of deciduous short shoots, and the abundance of Czekanowskiales at higher northern palaeolatitudes (Vakhrameev, 1978) suggests that this may be related to climatic seasonality. The Gnetales are very poorly represented in the megafossil record (Crane & Upchurch, unpublished) but are abundantly represented in palynofloras from tropical or arid areas (Brenner, 1976).

Barremian floras

Floristic provinces during the Barremian were similar to those of the Neocomian, and these Early Cretaceous floras are included together in the compilation of systematic data (Figure 5.2(*a*)). During the Barremian, or perhaps in the latest Neocomian, columellate semi-tectate pollen typical of flowering plants appears for the first time in palynofloras from southern England (Hughes, Drewry & Laing, 1979), Israel (Brenner, 1984), West Africa, Argentina and eastern North America (Hickey & Doyle, 1977). Although the abundance of angiosperm pollen in Barremian floras is typically less than 1 %, the systematic diversity may be considerable, and 15 kinds of presumed angiosperm pollen have been distinguished in the Barremian of southern England (Hughes *et al.*, 1979). In the Barremian of Gabon, sediments of the developing mid-Atlantic rift valley (Cocobeach sequence) that contain a diversity of monosulcate angiosperm pollen also have a high proportion of ephedroid grains relative to cheirolepidiaceous conifer pollen (Doyle, Jardiné & Doerenkamp, 1982), suggesting that early angiosperms initially colonized habitats in which these conifers were uncommon. Although there is geological evidence of aridity in the Barremian part of the Cocobeach sequence, angiosperm pollen occurs simultaneously in more equable areas (e.g. Israel, Sénégal), and thus there is no clear palaeontological support for the hypothesis (Stebbins, 1974) that angiosperms originated and diversified in seasonally arid environments (Doyle *et al.*, 1982).

Aptian and early Albian floras

During the mid-Cretaceous, Brenner (1976) recognized four floristic provinces on the basis of palynological assemblages: Northern Laurasia, Southern Laurasia, Northern Gondwana and Southern Gondwana

(Figure 5.1(*b*)). The Northern Laurasian province is broadly equivalent to the Jurassic–Neocomian Siberian–Canadian province, while the Southern Laurasian province corresponds approximately to the Euro-Sinian (Indo-European realm; Vakhrameev, 1975). Angiosperm leaves are not abundant in Aptian and early Albian floras. Where present they account for only about 5% of the species of leaf megafossils in floras of this age (Figure 5.2(*a*)). The percentage representation of cycadophytes and 'other' gymnosperm species in Aptian and early Albian floras decreases slightly with respect to Neocomian floras, while the percentage representation of pteridophytes and conifers shows a small increase.

Palynofloras from the Southern Laurasian and Northern Gondwanan provinces are more diverse than those from higher latitudes and contain angiosperm grains closely comparable to pollen of extant monocotyledons, the Chloranthaceae and Winteraceae (Walker, Brenner & Walker, 1983; Walker & Walker, 1984). Angiosperm pollen is most abundant and diverse in Northern Gondwana palynofloras, and in the Early Aptian of the Ivory Coast angiosperm pollen may account for over 10% of the pollen flora (Doyle *et al.*, 1982). Tricolpate pollen appears for the first time at around the Barremian–Aptian boundary in the Northern Gondwana province (Brenner, 1976; Doyle *et al.*, 1982), and this indicates the first appearance of the clade of non-magnoliid dicotyledons (subclasses Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae) that accounts for over 70% of extant angiosperm species (Cronquist, 1981). During the Aptian, tricolpate pollen is common in Northern Gondwana, but there are few, if any, tricolpate grains recorded from the Aptian of Southern Laurasia.

Northern Gondwana palynofloras are typically low in pteridophyte spores and bisaccate conifer pollen (Brenner, 1976), whereas the reverse is true in the Southern Laurasian province, where the Schizaeaceae, Gleicheniaceae, Pinaceae and Podocarpaceae are all well represented. *Classopollis* is abundant in both provinces, but the most striking feature of Northern Gondwana palynofloras is the abundance (up to 40%) of *Ephedra*-like pollen (Figure 5.2(*b*)), which may also include forms with horn-like or elater-like projections (e.g. *Galeacornea*, *Elaterosporites*). *Ephedra*-like pollen is much less conspicuous in Southern Laurasia palynofloras. In Northern Gondwana, *Ephedra*-like pollen diversified almost simultaneously with angiosperm pollen, and, during the Aptian, fluctuations in abundance seem to follow similar fluctuations in angiosperm pollen content (Doyle *et al.*, 1982). This is consistent with the limited evidence available from megafossils that at least some early

Cretaceous Gnetales and angiosperms occupied similar habitats (Crane & Upchurch, unpublished).

During the Aptian and early Albian, palynofloras in the Northern Laurasian province typically lack angiosperm pollen, *Classopollis* and *Ephedra*-like pollen is rare, and, with the exception of spores of some Osmundaceae, Northern Laurasia palynofloras include only a relatively small component of pteridophyte spores. The proportion of bisaccate conifer pollen is correspondingly higher.

Very few Aptian to early Albian megafossil floras contain abundant angiosperms. In the Potomac Group, approximately 12 different taxa have been recognized among leaves of this age (Upchurch, 1984*a*). Aptian and early Albian angiosperm leaves have poorly organized venation (Wolfe, Doyle & Page, 1975), and those studied in detail show features characteristic of extant Magnoliidae, particularly Magnoliales, Chloranthaceae and Illiciales (Upchurch, 1984*a*, *b*). The leaves are generally small (Vakhrameev, 1981; Upchurch & Wolfe, this volume, Chapter 4) and in the Potomac Group occur consistently in moderately coarse to medium-fine sands and silts interpreted as near channel and levee deposits (Hickey & Doyle, 1977). At some Potomac Group localities, stems with attached leaves provide direct evidence of herbaceous angiosperms (Hickey & Doyle, 1977; Upchurch, 1984*a*; Upchurch, Hickey & Niklas, 1983), and sedimentological evidence suggests that, together with ferns and herbaceous gnetaleans, these were early successional colonizers of disturbed habitats (Crane & Upchurch, unpublished). Angiosperm megafossils are absent from Northern Laurasia megafloras, and, although cycadophytes are generally sparse (Vakhrameev, 1971), *Nilssonia* foliage may be common in some assemblages.

Late Albian floras

In the late Albian, floristic provinciality was very similar to that in the Aptian and early Albian (Figure 5.1(*b*)), but the geographic spread of flowering plants, at least in the Northern Hemisphere, was essentially completed (Samylina, 1968). By this time angiosperm megafossils and pollen are an important component of northern high latitude floras in areas from which they were previously absent (e.g. western Canada; Bell, 1956; Singh, 1975; and north slope of Alaska; R. A. Spicer, personal communication). Angiosperm leaves typically account for 40% to 50% of the taxa described in late Albian megafloras, and this expansion in the relative importance of angiosperms corresponds to a marked decline in the importance of cycadophytes, other seed plants, and pteridophytes in floras of this age (Figure 5.2(*a*); see also Vakhrameev, 1978). The conifers are the group least affected by the angiosperm diversification.

Angiosperm pollen is significantly more abundant in late Albian than in early Albian palynofloras, and, in Northern Gondwana and Southern Laurasia, Aptian forms (e.g. *Clavatipollenites*) are joined by a variety of new angiosperm pollen types including monosulcate, tricolpate, tricolporate and periporate taxa (Muller, 1984). In the late Albian of the Potomac Group (Southern Laurasia), the relative abundance of tricolpate and tricolporate pollen grains may be as high as 70% at some localities (J. A. Doyle, personal communication). This increase in angiosperm pollen is accompanied, in the Potomac Group, by a slight decline in the abundance of schizaeaceous spores, *Classopollis* and *Exesipollenites* (probably pollen of Bennettitales; Harris, 1974), but there is a corresponding increase of *Araucariacites* and bisaccate conifer pollen (Brenner, 1963). At lower palaeolatitudes (Northern Gondwana), angiosperm pollen is more diverse, but palynofloras generally remained dominated by *Classopollis* and a variety of ephedroid grains (Figure 5.2(*b*); Muller, 1984). In Northern Laurasia, angiosperm pollen appears for the first time during the Albian, and monosulcate and tricolpate grains appear more or less synchronously (Singh, 1975).

Angiosperm leaves are much more diverse and abundant in the late Albian part of the Potomac Group (Southern Laurasia) than in the Aptian and early Albian, and it is estimated that about 36 different kinds are represented (Doyle & Hickey, 1976). Angiosperm leaves are locally dominant in some floras of this age and may account for almost all of the megafossils collected (e.g. West Brothers locality; Hickey & Doyle, 1977). Systematically angiosperm leaves, reproductive structures, and pollen from the late Albian part of the Potomac Group clearly demonstrate the presence of monocotyledons, magnoliids, hamamelidids and rosids (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Upchurch, 1984*a*, *b*; Crane, Friis & Pedersen, 1986; Friis, Crane & Pedersen, 1986).

In addition to exhibiting increased systematic diversity, angiosperms had also attained considerable ecological amplitude by the end of the Early Cretaceous (Samylina, 1968). Late Albian leaves are generally larger, structurally more complex, and have more highly organized venation than those in the Aptian and early Albian. Evidence from functional morphology and sedimentology indicates that this increased variety of leaf morphologies reflects a major ecological radiation, during which angiosperms became established not only in early successional

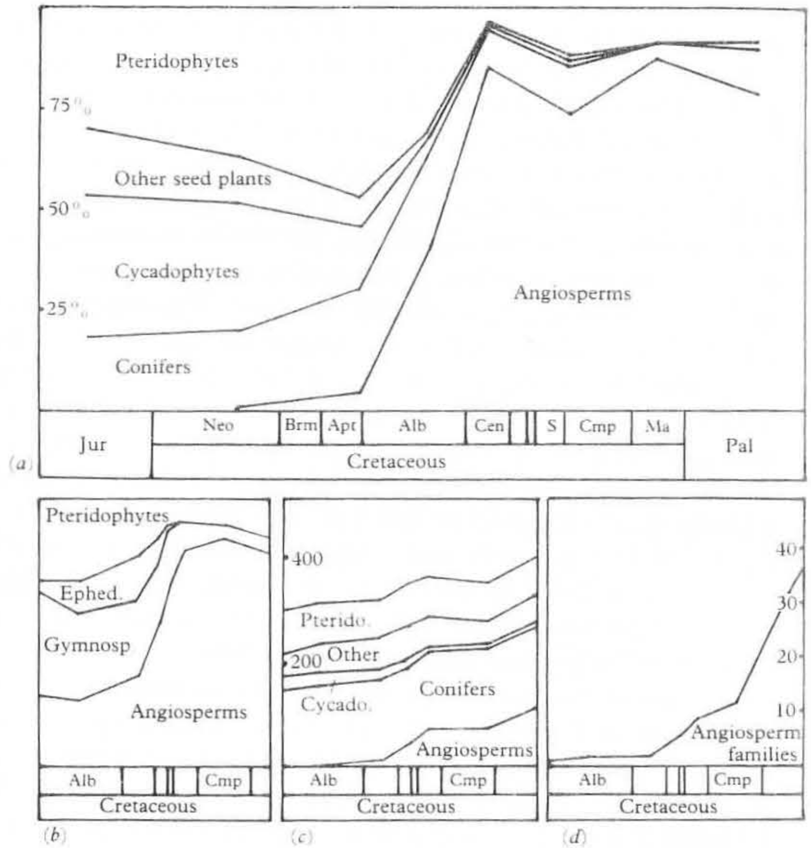

Figure 5.2. Estimates of the timing and magnitude of the angiosperm radiation. (*a*) Changes in mean percentage contribution of major plant groups to Jurassic (Jur), Cretaceous and Paleocene (Pal) floras. Calculated from mean species numbers in Jurassic–Paleocene floras listed in Appendix. Pteridophytes (Pterido.) include ferns and lycopods; cycadophytes (Cycado.) include cycads, Bennettitales and pinnate-leaved seed ferns. Identical major patterns of change are obtained if percentages are calculated from genera, or if mean species or mean genus numbers are used without conversion into percentages. Neo, Neocomian; Brm, Barremian; Apt, Aptian; Alb, Albian; Cmp, Campanian; Cen, Cenomanian; S, Santonian; Ma, Maastrichtian. (*b*) Percentage contribution of 'species' of major plant groups to Cretaceous palynofloras. The percentage of ephedroid (Ephed.) species is based on palynomorphs of the *Galeacornea* group. (Based on microfloral diversity curves for South America and Africa (Muller, 1984, Fig. 2).) (*c*) Estimated absolute species diversity of major plant groups between the Jurassic and the

habitats, but also as full aquatics and riparian trees (Doyle & Hickey, 1976; Hickey & Doyle, 1977). *Sapindopsis* and platanoid leaves that are particularly abundant at several Potomac Group localities and elsewhere in the Northern Hemisphere are interpreted as being plants of early successional angiosperm thickets. In the Potomac Group, conifers and Bennettitales are thought to have remained dominant in backswamp areas throughout the Albian (Hickey & Doyle, 1977).

Cenomanian floras

In the Cenomanian, floristic provinciality is very similar to that in the Aptian and Albian (Figure 5.1(*b*)). Angiosperms consistently dominate megafossil floras on a global scale for the first time, although locally, as in floras of this age from Czechoslovakia, gymnosperms may remain diverse (Velenovský & Viniklář, 1926, 1927, 1929, 1931; Pacltová, 1977). Angiosperm leaves typically account for about 75 % of the taxa described from Cenomanian megafloras, and their systematic representation remains at this level throughout the Late Cretaceous and into the Early Tertiary. The percentage representation of conifer taxa in Cenomanian floras is about half of that in Neocomian floras (approximately 15 %), but cycadophytes, pteridophytes and 'other' seed plants exhibit much more dramatic declines and generally only account for about 2 %, 6 % and 1 % of the megafossil taxa per flora, respectively (Figure 5.2(*a*)).

At low palaeolatitudes (Northern Gondwana), angiosperm pollen accounts typically for about 50 % of the total number of the dispersed palynomorph species (Muller, 1984), although some palynofloras may still be dominated by ephedroid and *Classopollis* pollen (Figure 5.2(*b*)). At middle and high palaeolatitudes, the abundance of angiosperm pollen varies considerably, but, even at megafossil localities that are dominated by angiosperm leaves, the relative abundance of angiosperm pollen may be only about 25 % (Penny, 1969). Other palynofloras are dominated by angiosperms, the remaining palynomorphs consisting largely of saccate pollen of probable Pinaceae and Podocarpaceae, and inaperturate pollen of probable Taxodiaceae. The angiosperm component of Cenomanian palynofloras is more diverse than in the Albian, and in particular there is a considerable variety of tricolpate, tricolporoidate and tricolporate

Paleocene. (Based on Niklas *et al.*, 1985, Fig. 3.) (*d*) First appearances of extant angiosperm families during the Cretaceous and the Paleocene, on the basis of fossil pollen (data from Muller, 1981, Table II). Families first recorded at the boundary between two stages were treated as appearing within the younger stage.

taxa. Triporate pollen grains appear for the first time in the Middle Cenomanian of Europe and North America (Southern Laurasia; Laing, 1975; Pacltová, 1978; Doyle & Hickey, 1976) and begin to diversify rapidly toward the end of this stage. Triporate pollen such as *Complexiopollis* are some of the earliest representatives of the Normapolles group, later members of which are known to be related to extant Juglandales (Friis, 1983), and perhaps other 'Amentiferae' such as Betulaceae and Myricaceae. Although some Normapolles grains may have been dispersed by insects (Batten, 1984), the size and lack of sculpture on most early representatives is consistent with wind pollination.

The diversity of angiosperm leaves in Cenomanian floras far exceeds that known from Albian floras. Magnoliid taxa are widespread (e.g. the *Myrtophyllum* and *Cocculophyllum* groups of Kvaček (1983)), but typically even these Cenomanian magnoliids have more highly organized venation than do their Aptian counterparts (G. R. Upchurch, personal communication). Conclusions based on leaves are therefore consistent with both floral and palynological data, which indicate that magnoliids had undergone a major radiation by the end of the Cenomanian. In addition, many Cenomanian leaf floras are dominated by a wide variety of platanoid taxa and related hamamelidids (e.g. the *Platanus–Credneria* and *Aralia–Debeya* groups of Kvaček (1983)). In the Early Cenomanian of central Kansas most of the leaves from the Dakota Sandstone Flora that have been assigned to *Aralia*, *Betulites*, *Platanus*, *Sassafras* and *Viburnum* (cf. Berry, 1916) belong to this highly variable platanoid–hamamelidid group. Most of the 'Dakota Sandstone' represents probable channel and levee sands (Retallack & Dilcher, 1981), and the abundance of platanoid leaves in such environments recalls the streamside habit of extant *Platanus*.

Turonian–Campanian floras

During the Turonian–Campanian, the angiosperm component of most eastern North American and European palynofloras is dominated by oblate triporate grains, frequently with complex compound apertures (Normapolles pollen). This Normapolles province (Figure 5.1(*c*)) corresponds approximately to the mid-Cretaceous southern Laurasian province and is apparently delimited to the north and south by climatic boundaries (see Upchurch & Wolfe, this volume, Chapter 4). Although Normapolles pollen does occasionally occur outside its characteristic range (e.g. California, China, India), the major abundance and diversity is longitudinally delimited by epicontinental seas (Batten, 1984). Within the Normapolles province, the eastern North American and European sub-provinces had different compositions, with the greatest variety of Normapolles forms being recorded from Europe (Batten, 1981). To the north of the Normapolles province the *Aquilapollenites* province (Figure 5.1(*c*)) is approximately equivalent to the mid-Cretaceous Northern Laurasian province, and has diverse palynofloras characterized by taxa such as *Aquilapollenites*, *Triprojectus*, *Wodehouseia* and *Proteacidites* (Norris, Jarzen & Awai-Thorne, 1975; Batten, 1984). Although *Aquilapollenites* shows some similarities to pollen of Santalales (Jarzen, 1977), the systematic relationships of these grains are poorly understood.

During the Turonian–Campanian, as in the Cenomanian, angiosperms account for approximately 70% of the species recorded in megafossil floras (Figure 5.2(*a*)). Pteridophytes and conifers each account for about 10%, while cycadophytes are usually very poorly represented (but see below).

In low palaeolatitude palynofloras (Northern Gondwana) angiosperms account typically for about 54% of the total palynomorph species in the Turonian, rising to 70% and 85% in the Coniacian and Campanian, respectively (Figure 5.2(*b*); Muller, 1984). By the Campanian, the considerable mid-Cretaceous diversity of *Ephedra*-like pollen had almost completely disappeared. In the Normapolles province, palynofloras are usually dominated by angiosperms, but at higher palaeolatitudes (*Aquilapollenites* province) angiosperms were less abundant relative to gymnosperms (Jarzen & Norris, 1975). In the Oldman Formation (southern Alberta, Campanian) the relative abundance of angiosperms is typically about 30% to 40% of the pollen flora, while gymnosperms account for 15% to 20% and ferns about 30% (Jarzen, 1982*b*). In terms of the diversity of palynomorph 'species', angiosperms account for only 43% of the species recognized. Pteridophyte and bryophyte spores account for 38%, while gymnosperm pollen accounts for 24% (Jarzen 1982*b*). Megaspores are diverse and abundant in some floras (e.g. Knobloch, 1984), suggesting that both lycopods and water ferns may have been important herbs at this time.

Cycadophytes are very poorly represented in most Turonian–Campanian floras, but occur sporadically (Berry, 1929) and persisted in greater numbers at high palaeolatitudes (Krassilov, 1975, 1983). In the Nanaimo flora (Vancouver Island; Bell, 1957), there are three genera of cycadophytes representing cycads, pteridosperms, and Bennettitales, but no numerical data are available to estimate their abundance in the vegetation. However, in the Mgachi flora (North Sakhalin; Krassilov, 1978), where cycads also occur, they account for less than 2% of the megafossil collection. The seed fern *Sagenopteris* (leaf of the *Caytonia* plant) also accounts for less than 2% of the plants collected, and both groups were probably only a minor component of the vegetation. The Mgachi flora is dominated by conifers (70% recorded megafossils) and indicates a conifer forest with an understory of angiosperms and ferns (Krassilov, 1978).

During the Turonian–Campanian interval, the number of angiosperms clearly related to extant groups at the ordinal level or below increases, and, by the Campanian, Muller (1981) recognized 13 orders and 12 families of extant angiosperms. As in the Cenomanian, it is the Magnoliidae, Hamamelididae and Rosidae that are best represented. In the middle and late Cretaceous, leaves related to the platanoid complex (*Debeya*, e.g. Němejc & Kvaček, 1975; *Dewalquea*, e.g. Knowlton, 1918) show features suggestive of a relationship to extant Fagaceae (Rüffle, 1977). Angiosperm reproductive remains of this age (Knobloch & Mai, 1984; Friis, 1985) can usually be assigned to a specific extant family or group of families. Normapolles grains (*Plicapollis*, *Trudopollis*) recorded from fossil flowers clearly demonstrate that at least some Normapolles were related to extant Juglandales (Friis, 1983). Palms also became important for the first time during the Turonian–Campanian interval, particularly at low palaeolatitudes and palm leaves and stems of probable Coniacian age are recorded from eastern North America (Daghlian, 1981).

Maastrichtian floras

During the Maastrichtian, floristic provinciality and the diversity and abundance of major plant groups is very similar to that of the Campanian (Figures 5.1(*c*), 5.2(*a*)). Angiosperms, however, appear to undergo a major modernization, with an approximate doubling of the number of extant families and orders recognizable on the basis of dispersed pollen (Figure 5.2(*d*); Muller, 1981). There is palynological evidence of all of the dicotyledonous subclasses except the Asteridae by the close of the Maastrichtian (Muller, 1981), palm pollen is common and diverse, and triporate pollen closely similar to that of extant Betulaceae, Juglandaceae, and Myricaceae is increasingly abundant.

In both the megafossil and palynological record, the Taxodiaceae are the most abundant and widespread conifers at higher palaeolatitudes, whereas at lower palaeolatitudes the Araucariaceae and Podocarpaceae are more common. With the exception of high latitude areas and conifer swamps, conifers rarely dominate the angiosperms during the Maastrichtian. Of the 12 localities in the Fox Hills, Lower Medicine Bow and Lance floras assessed quantitatively by Dorf (1942), only two are dominated by conifers. In middle and low palaeolatitude areas of the Northern Hemisphere corresponding to the Northern Gondwana and Normapolles provinces, megafossil floras contain a preponderance of leaves of probable Euphorbiaceae, Illiciales, Laurales and palms (Wolfe & Upchurch, unpublished; see also Bande, Prakash & Ambwani, 1981).

In the *Aquilapollenites* province, the megafossil floras are dominated by several characteristic Paleocene groups, including the *Nyssidium*/*Joffrea* lineage related to extant *Cercidiphyllum* (Brown, 1939; Crane, 1984), the *Nordenskioldia* lineage, probably related to extant *Trochodendron* and *Tetracentron*, as well as probable Trochodendrales, Platanaceae, Juglandaceae and Betulaceae (Shoemaker, 1966).

Paleocene floras

The large number of Paleocene megafloras from the Northern Hemisphere are generally rather uniform, particularly at middle to high palaeolatitudes (cf. Brown, 1962; Krassilov, 1976). Palynologically, however, in the area approximately corresponding to the mid-Cretaceous Northern and Southern Laurasian provinces and the Late Cretaceous Normapolles and *Aquilapollenites* provinces, Krutzsch (1967) has recognized a North Atlantic European province, including Europe, eastern North America and Greenland, and a Siberian–Pacific province including western North America, Asia and Australasia (Figure 5.1(*d*)). In terms of the relative abundance and diversity of major plant groups, Paleocene floras resemble those of the Maastrichtian (Figure 5.2(*a*)).

Further, apparently rapid modernization of the angiosperm flora occurs during the Paleocene, and the number of extant families recognized from dispersed pollen doubles from the Maastrichtian level (Figure 5.2(*d*); Muller, 1981). Triporate pollen is frequently very abundant in Paleocene palynofloras, particularly at middle and high palaeolatitudes (e.g. Zaklinskaya, 1967; Kedves, 1982), and contemporaneous megafossils indicate the presence of extinct Betulaceae and Juglandaceae (Crane, 1982; Manchester, 1987). Compared to those from the Upper Cretaceous, Paleocene palynofloras in these areas are relatively impoverished (Leffingwell, 1970; Tschudy, 1970), and estimates of extinction across the Cretaceous–Tertiary boundary based on megafossils vary from 40% to 75% (Hickey, 1981; Wolfe & Upchurch, unpublished). In areas approximately corresponding to the earlier Southern Laurasian and Normapolles provinces, Paleocene floras are typically dominated by palms and entire-margined leaves of the Euphorbiaceae and Laurales, many of which were apparently evergreen (Wolfe & Upchurch, unpublished). Serrate-margined leaves are probably assignable to the Juglandaceae and Tiliaceae, and, toward the end of the Paleocene, leaflets of the Leguminosae are common. Conifers are generally rare and herbs are represented by a variety of ferns.

At higher palaeolatitudes, the characteristic Paleocene conifers are probably deciduous Taxodiaceae (*Glyptostrobus*, *Metasequoia*, *Parataxodium*), and the typical ferns include *Lygodium*, *Onoclea* and *Dennstaedtia* (Brown, 1962; Hickey, 1977). The last records of characteristic Neocomian cycadophytes and ferns occur in high latitude Paleocene floras from Alaska (Hollick, 1936). The commoner angiosperms include Betulaceae and Platanaceae. Reproductive structure of the extinct species in the *Cercidiphyllum/Nyssidium/Joffrea* lineage and Platanaceae demonstrates that these plants may have been important opportunistic colonizers in the Paleocene vegetation (Crane & Stockey, 1985; Manchester, 1986), and this is strongly supported by the occurrence of large numbers of even-aged seedlings of both taxa over large areas (Stockey & Crane, 1983). In view of the apparent scarcity of angiosperm herbs at this time, it is possible that opportunistic shrubs fulfilled a more important role in the colonization of bare ground than in many present-day plant communities. Lianes may also have been effective early colonizers, as in disturbed tropical vegetation today (R. A. Spicer, personal communication), and this may account for the abundance of families such as the Menispermaceae and Vitaceae in many Early Tertiary floras (e.g. Reid & Chandler, 1933; Chandler, 1961; but see also Upchurch & Wolfe, this volume, Chapter 4; Collinson & Hooker, this volume, Chapter 10). The ubiquity of megaspores in Paleocene floras (e.g. Melchior & Hall, 1983) also suggests that lycopods may have been important contemporaneous herbs.

Vegetational consequences

Community composition

Analyses of the mean number of species of major plant groups in Jurassic, Cretaceous and Paleocene floras show clearly that, as the angiosperms increase, the mean number of cycadophytes, other seed plant and pteridophyte species abruptly declines (Figure 5.2(*a*)). Cretaceous megafossil sequences in Alaska (Smiley, 1972) and New Zealand (McQueen, 1956) that were not included in the data compilation show an almost identical pattern. The decrease in the mean number of conifer species per flora is small, although there are marked qualitative changes in the conifers present. The Cheirolepidiaceae are of much less importance in Late Cretaceous floras, while in the palynological record, at least at middle palaeolatitudes, there is a trend toward increasing abundance of pollen of probable Araucariaceae, Pinaceae, Podocarpaceae and Taxodiaceae (Doyle, 1977).

Analyses of species ranges in mid-Cretaceous floras from eastern North America show high levels of local extinction and systematic replacement for all major groups (Dorf, 1952; see also Vakhrameev, 1971). Pteridophytes and gymnosperms both play a more minor role in Late Cretaceous floras than in Early Cretaceous floras. This pattern is not reflected in recent estimates of global plant diversity through the Cretaceous (Niklas, Tiffney & Knoll, 1985), which show only minor declines in pteridophytes and cycadophytes, and a slow increase in angiosperm diversity (Figure 5.2(*c*)). Although the persistence of some typical Neocomian gymnosperms and pteridophytes in Paleocene high latitude floras will tend to preserve high levels of global diversity for these groups (cf. Krassilov, 1983), the estimate of angiosperm diversity is anomalously low (compare Figures 5.2(*a*),(*c*)). Analyses of mid-Cretaceous megafossil floras indicate that angiosperms were diverse and attained major importance in a variety of plant communities during the Cenomanian. Cenomanian floras from a variety of depositional settings are dominated by angiosperm leaves (Retallack & Dilcher, 1981; and see Appendix, p. 129), and, within the limitations common to most plant fossil assemblages, this does not appear to be an effect of biased palaeoenvironmental sampling. In the palynological record, however, angiosperm dominance is less clear. On the basis of analyses of palynomorph 'species' diversity in different low palaeolatitude areas, Muller (1984) concluded that the angiosperm 'ecological breakthrough' was not completed until the Turonian, and analyses of the relative abundance of pollen and spores in Cenomanian palynofloras from middle palaeolatitudes, show that angiosperms account typically for only about 40% to 60% of the dispersed palynomorphs. Underrepresentation of angiosperms in the palynoflora may suggest that uplands and well-drained areas remained dominated by conifers in the early Late Creceous, but could also result from the preponderance of insect-pollinated taxa in the earlier phases of the flowering plant radiation (Friis & Crepet, this volume, Chapter 6; Crepet & Friis, this volume, Chapter 7) and the probable lauralean affinities of many mid-Cretaceous magnoliid angiosperms

(G. R. Upchurch, personal communication). Pollen of most extant Laurales has a very thin sporopollenin exine, which is rarely preserved in the fossil record. The seemingly anomalous low diversity of angiosperm pollen in the Cenomanian may reflect palynological uniformity among early angiosperms, and in particular the practical difficulties of discriminating between the small tricolpate and tricolporoidate pollen grains that were probably produced by a variety of early representatives of the Hamamelididae and Rosidae (Doyle & Hickey, 1976; Crane *et al.*, 1986).

Although the marked declines in local importance of cycadophytes and pteridophytes that occurred as a result of the angiosperm radiation could be taken as evidence of competition between angiosperms and other tracheophytes, potential explanations for the success of flowering plants (e.g. Regal, 1977) are difficult to test with the data currently available. All of the major families of Jurassic and Early Cretaceous ferns become much less important in Late Cretaceous floras, and in particular there is a marked decline in the abundance of schizaeaceous spores (Brenner, 1963). Under certain circumstances Recent ferns and lycopods may be highly effective colonizers of bare ground (Spicer *et al.*, 1985), and families such as the Schizaeaceae and Gleicheniaceae, which probably dominated open environments at middle palaeolatitudes during the Early Cretaceous, may have been quickly affected by the appearance of opportunistic herbaceous or shrubby seed plants. Initially, middle palaeolatitude fern-savannas may have been replaced by angiosperm-fern-gnetalean communities, until the Gnetales themselves almost became extinct. Today the extant representatives of the characteristic Mesozoic fern families play a minor vegetational role compared to that of the 'higher' filicalean ferns (e.g. Polypodiaceae *sensu lato*) that diversified more recently, both figuratively and literally, in the shadow of the angiosperms. The correlation between extant ferns and damp shaded habitats may therefore have as much to do with the evolution of flowering plants as the biological limitations of pteridophytic reproduction (see also Upchurch & Wolfe, this volume, Chapter 4).

The most dramatic effect of the angiosperm radiation was on the cycadophytes (Figure 5.2(*a*)). The Bennettitales and pinnate-leaved seed ferns eventually became extinct, while the cycads became less diverse and more restricted in distribution. At middle palaeolatitudes these changes were more or less complete by the end of the Cenomanian (for an alternative view, see Krassilov, 1983). The demise of the Bennettitales is of particular interest because, like the Gnetales, many aspects of their reproductive biology were apparently similar to that of angiosperms, and this may have accentuated the competition between these groups. Angiosperms may not, therefore, have moved unchallenged into their role as the predominant early successional seed plants (cf. Tiffney, 1984), and at least some of the biological similarities of the angiosperms, Bennettitales and Gnetales may have been inherited from their common ancestor (Crane, 1985).

Community structure

Against the background of the major compositional and geographic changes in mid-Cretaceous vegetation there are some indications of an ecological pattern to the angiosperm radiation. Conclusions based on the Potomac Group need to be tested in other areas, but indicate that angiosperms first became established as early successional herbs or shrubs in disturbed habitats (Doyle & Hickey, 1976; Crane & Upchurch, unpublished). In particular, sedimentological data suggest that early angiosperms may have been important stream-side weeds in areas recently disturbed by erosion and deposition. During the late Albian, in the Potomac Group, angiosperms apparently diversified ecologically to occupy stream-side and aquatic habitats, the forest understory and early successional thickets (Doyle & Hickey, 1976; Hickey & Doyle, 1977). The average seed volume of around 1 mm^3 in Late Cretaceous angiosperms may have limited establishment to open conditions in which seedling photosynthesis could proceed unhindered (Tiffney, 1984). However, the stage at which angiosperms attained the status of dominant, canopy-forming large trees is more difficult to establish (see also Upchurch & Wolfe, this volume, Chapter 4). Among the largest angiosperm woods so far recorded from the Cretaceous are *Hythia* and *Cantia* from the Early Aptian and Early Albian, respectively (Stopes, 1915); however, there is controversy over the age of these specimens (Hughes, 1976), and most Late Cretaceous angiosperm woods are typically less than 10 cm in diameter (e.g. Page, 1979) in contrast to the large stumps of Mesozoic conifers (e.g. Bannan & Fry, 1957).

If the paucity of large fragments of fossil angiosperm wood reflects a scarcity of large arborescent dicotyledons (Upchurch & Wolfe, this volume, Chapter 4) it could support the view that Late Cretaceous angiosperms were ecologically subservient to gymnosperms and occupied only 'marginal or open habitats in the gymnosperm dominated vegetation' (Tiffney, 1984; see also Krassilov, 1983). However, even given the palaeoenvironmental bias toward lowland vegetation of most plant fossil assemblages, this hypothesis is difficult to reconcile with the

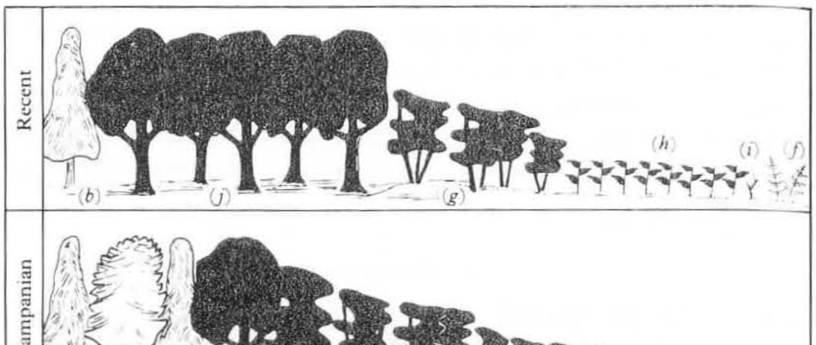

Figure 5.3. Diagram summarizing the distribution of major plant groups between major life-form categories for Neocomian, Aptian, Cenomanian, Campanian and Recent mid-latitude vegetation. (a), araucarian conifer; (b), taxodiaceous conifer; (c), cycadophyte shrub; (d), *Cycadeoidea* type bennettitalean; (e), herbaceous lycopod; (f), fern; (g), angiosperm shrub; (h), angiosperm herb; (i) gnetalean herb or small shrub; (j), angiosperm tree.

diversity and abundance of angiosperm megafossils, and the relative paucity of gymnosperms, in Late Cretaceous fossil floras (cf. Vakhrameev, 1981). A possible alternative scenario for mid-palaeolatitude vegetation is that small angiosperm trees or shrubs were sufficiently effective colonizers to exclude gymnosperms from most lowland habitats except perhaps taxodiaceous swamp forests. The result would be considerable areas dominated by shrubs or small trees (cf. the Mesozoic chaparral of Krassilov, 1973*a*), in which large arborescent angiosperms were uncommon and from which conifers such as Araucariaceae or Taxodiaceae were largely excluded or confined to occasional emergents. Other conifers (e.g. *Cephalotaxus*, *Torreya*) may themselves have been small trees or shrubs (Krassilov, 1973*b*). The hypothesized absence of large angiosperm trees during the mid-Cretaceous may lead to a misinterpretation of the effects of differential decay of angiosperm and conifer wood, and requires detailed examination, but it is apparently consistent with the observation, based on dinosaur remains, that during the Campanian (Dinosaur Provincial Park, Alberta) 'most of the primary productivity consumed by large herbivores must have been located between 0.5 and 4.0 m off the ground' (Béland & Russell, 1978; see also Coe *et al.*, this volume, Chapter 9).

The probable major changes in the structure and composition of terrestrial plant communities during the Cretaceous are summarized in Figure 5.3. The available evidence indicates that angiosperms first became established as early successional weedy herbs or shrubs, colonizing predominantly open environments or, at middle palaeolatitudes, habitats previously occupied by ferns and lycopods. Angiosperm small trees and shrubs that diversified very early in the Late Cretaceous may also have been highly effective colonizers, and apparently expanded first to dominate environments previously occupied by cycadophytes. Assuming appropriate climatic conditions (Upchurch & Wolfe, this volume, Chapter 4), close spacing of widely distributed small trees or shrubs would have provided ideal conditions for the development of wind pollination in the mid-Cenomanian. Compared to cycadophytes and pteridophytes, the relative abundance of conifers was little affected by the angiosperm radiation, and conifers are the only group of gymnosperms to have maintained their dominance over large areas in the face of competition from angiosperms (Regal, 1977). Large canopy-forming angiosperm forest trees may not have become widespread until the latest Cretaceous or Early Tertiary. The radiation of the major groups of extant angiosperm herbs, which account for about half of the number of extant angiosperm species (Van Valen, 1973), did not take place until later in the Tertiary.

Community stability and change

The increasing modernization of the angiosperm flora from the mid-Cretaceous is well documented by palynological evidence (Muller, 1984), and accumulating information from megafossils suggests that the available curves (Figure 5.2(*d*)) may even underestimate the extent to which Cretaceous angiosperms can be placed in extant families and orders (cf. Knobloch & Mai, 1984; Friis, 1985; Friis *et al.*, 1986). In parallel with this increasing modernization, is it possible to trace the history of Recent plant communities in the fossil record? For many years plant ecologists interpreted climax plant communities as 'super organisms' with their own 'growth and development' and 'ontogeny and phylogeny' (Clements, 1949, p. 123). The palaeobotanical manifestation of Clementsian ecology is the concept of the geoflora as 'a group of plants that has maintained itself with only minor changes in composition for several periods of earth history' (Chaney in Chaney & Axelrod, 1959, p. 12). In the latest Cretaceous and Early Tertiary of the Northern Hemisphere, two major geofloras have been recognized traditionally. North of about 40° Paleocene palaeolatitude, the 'Arcto-Tertiary Geoflora' consisted of 'the group of temperate plants which is recorded in the older Tertiary rocks of Greenland, Spitzbergen, Alaska and arctic Canada, and which has spread southward through Eurasia and North America during the Cenozoic' (Chaney in Chaney & Axelrod, 1959, p. 12). The Arcto-Tertiary Geoflora is more or less equivalent to the Paleocene Greenland, and Eocene–Oligocene Turgaian Provinces of Krystofovich (1955), and has been interpreted as the once widespread precursor of the now more restricted 'mixed mesophytic forest' of eastern Asia and eastern North America (Wang, 1961). The more southerly Neotropical, or Palaeotropical, Geoflora consisted mainly of tropical evergreen dicotyledons, notably the Lauraceae, and is broadly equivalent to the Paleocene Gelinden, and Eocene–Oligocene Poltavian Provinces of Krystofovich (1955), and the Mastixioidean flora of European Eocene and Oligocene brown coals (Kirchheimer, 1957).

Although the geoflora concept dominated a generation of floristic work on Early Tertiary floras (e.g. Chaney, 1940), improved systematic and stratigraphic interpretation suggest that it is a potentially misleading oversimplification. For example, Paleocene 'Arcto-Tertiary' floras are highly depauperate compared to Recent mixed mesophytic forest (Wolfe,

1977) and also include a large proportion of extinct genera (cf. Crane & Stockey, 1985). Similarly, the extensively studied 'Palaeotropical' London Clay flora contains a mixture of plants that have their nearest living relatives in tropical southeast Asia (e.g. *Nipa*), as well as the mixed mesophytic forest of east central China (e.g. *Platycarya*, c.f. also Chaney, 1949). Although the geoflora concept correctly emphasizes the systematic homogeneity of higher-latitude Northern Hemisphere vegetation during the earliest Tertiary, recent studies on individual angiosperm lineages suggest that the history of extant plant communities is too complex to be usefully simplified in this way. This is particularly true during the Tertiary where increasing continental dispersion (Smith, Hurley & Briden, 1981; McKenna, 1983) and climatic changes (Wolfe, 1975, 1978) eventually led to a major increase in both diversity and floristic provinciality. A more detailed understanding of the development of Recent plant communities seems more likely to emerge from studies of individual plant lineages in conjunction with independent assessments of palaeoenvironmental change.

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Appendix: List of Jurassic to Paleocene megafloras from the Northern Hemisphere

This list shows the number of species assigned to five major plant groups (not inclusive of reproductive structures or stems). Form genera (e.g. *Dicotylophyllum*) are treated as genera and varieties are treated as distinct species. Pteridophytes include lycopods and ferns; cycadophytes include cycads, Bennettitales and seed ferns with pinnate leaves; other seed plants include taxa such as *Baiera*, *Czekanowskia* and *Ginkgo* that are neither clearly cycadophytes nor conifers. The name of the flora is followed by the reference from which the counts of species were made. Sources for age determinations are given in parentheses only if different from, or more specific than, the source of systematic data.

1, Boroldaisky, USSR (Dolundenko & Orlovskaya, 1976); Middle Jurassic. 2, Borolsaisky, USSR (Dolundenko & Orlovskaya, 1976); Upper Jurassic. 3, Issyktasky, USSR (Dolundenko & Orlovskaya, 1976); Middle Jurassic. 4, Karabastausky, USSR (Dolundenko & Orlovskaya, 1976); Upper Jurassic. 5, Oregon, USA (Fontaine, in Ward, 1905); Upper Jurassic (J. A. Doyle, personal communication). 6, Oroville, USA (Ward, 1900); Upper Jurassic (J. A. Doyle, personal communication). 7, Yorkshire, UK (Harris, 1961*a*, 1964, 1969, 1979; Harris *et al.*, 1974); Middle Jurassic. 8, Hazelton, Canada (Bell, 1956); Neocomian–Barremian (restricted to plants from localities in the Hazelton–Cedarville area). 9, Horsetown, USA (Berry, 1911); Berriasian–Barremian (Hughes, 1976). 10, Kootenay, Canada (Bell, 1956); Berriasian (Stott, 1975). 11, Nikanassin, Canada (Bell, 1956); Berriasian (Stott, 1975). 12, Wealden, Germany (Berry, 1911); Neocomian (Hughes, 1976). 13, Wealden, Saxony (Berry, 1911); Neocomian (Hughes, 1976). 14, Wealden, U.K. (Berry, 1911); Neocomian (Hughes, 1976). 15, Upper Knoxville, USA (Berry, 1911); Neocomian (Hughes, 1976). 16, Almargem, Portugal (Teixeira, 1948); Aptian (Hughes, 1976). 17, Bullhead, Canada (Bell, 1956); Barremian–Aptian (Stott, 1975). 18, Cercal, Portugal (Teixeira, 1948); Upper Aptian–Lower Albian (Rey, 1972). 19, Fuson, USA (Berry, 1911); Aptian–Albian (McGookey *et al.*, 1972). 20, Kome, Greenland (Heer, 1893); Barremian–Aptian (K. R. Pedersen, personal communication). 21, Kootenai, USA (La Pasha & Miller, 1984); Aptian. 22, Lower Blairmore, Canada (Bell, 1956); Aptian–Lower Albian (Stelk, 1975; Stott, 1975). 23, Luscar, Canada (Bell, 1956); Aptian. 24, Potomac Group, Zone I, USA (based on lists given by Berry (1911) for the Baltimore, Dutch Gap, Fredericksburg, Potomac Run and Trent's Reach localities); Aptian–Lower Albian (Brenner, 1963; Doyle & Hickey, 1976). 25, Buarcos, Portugal (Teixeira, 1948); Albian (Hughes, 1976). 26, Cheyenne, USA (Berry, 1921*b*); Albian (Ward, 1983). 27, Kingsvale, Canada (Bell, 1956); Albian. 28, Nazaré, Portugal (Teixeira, 1948); Albian (Hughes, 1976). 29, Pasayten, Canada (Bell, 1956); Albian. 30, Potomac Group, Zone II, USA (based on lists given by Berry (1911) for the Deep Bottom, Mount Vernon, Stump Neck, Welhams, Whitewater and Whitehouse Bluff localities); Middle–Upper Albian (Brenner, 1963; Doyle & Hickey, 1976). 31, Taverede, Portugal (Teixeira, 1948); uppermost Albian–Cenomanian (Hughes, 1976). 32, Upper Blairmore, Canada (Bell, 1956); Albian (Stott, 1975). 33, Bingen, USA (Berry, 1917); Cenomanian (?coeval with Raritan). 34, Dakota, USA (Berry, 1916); Cenomanian (Hickey & Doyle, 1977). 35, Dunvegan, Canada (Bell, 1963); Cenomanian (Stott, 1975). 36, Kaltag, Alaska, USA (Hollick, 1930); Cenomanian (R. A. Spicer, personal communication). 37, Melozi, Alaska, USA (Hollick, 1930); Cenomanian (R. A. Spicer, personal communication). 38, Nulato, Alaska, USA (Hollick, 1930); Cenomanian (R. A. Spicer, personal communication). 39, Raritan, USA (based on the lists given by Newberry (1895) for the Woodbridge and Sayreville localities); Cenomanian (Christopher, 1979). 40, Tuscaloosa, USA (Berry, 1919); Cenomanian (Hazel *et al.*, 1977). 41, Woodbine, USA (Berry, 1921*a*); Cenomanian (Hedlund, 1966). 42, Atane, Greenland (Heer, 1893); Turonian–Santonian (K. R. Pedersen, personal communication). 43, Black Creek, USA (Berry, 1914); Santonian–Campanian (Hazel *et al.*, 1977). 44, Eutaw, USA (Berry, 1925); Coniacian–Santonian (Hazel *et al.*, 1977). 45, Frontier, USA (Knowlton, 1918); Cenomanian–Turonian (Nichols & Jacobson, 1982. 46, Fruitland & Kirtland, USA (Knowlton, 1917*a*); Campanian (McGookey *et al.*, 1972). 47, Judith River, USA (Knowlton, in Stanton & Hatcher, 1905); Campanian (McGookey *et al.*, 1972). 48, Magothy, USA (Berry. 1916); Coniacian–Santonian (Christopher, 1979). 49, Milk River, Canada (Bell, 1963); Santonian (Stelk, 1975). 50, Nanaimo, Canada (Bell, 1957); Coniacian–Campanian. 51, Patoot, Greenland (Heer, 1893); Santonian–Campanian (K. R. Pedersen, personal communication). 52, Dawson Arkose, USA (Knowlton, 1930); Maastrichtian (?coeval with Raton Formation). 53, Lance, USA (Dorf, 1942); Maastrichtian (McGookey *et al.*, 1972). 54, Laramie, USA (Knowlton, 1922); Maastrichtian (McGookey *et al.*, 1972). 55, Lower Edmonton, Canada (Bell, 1949); Maastrichtian. 56, Lower Medicine Bow, USA (Dorf, 1942); Maastrichtian (McGookey *et al.*, 1972). 57, Raton, USA (Knowlton, 1917*b*); Maastrichtian (McGookey *et al.*, 1972). 58, St Mary River, Canada (Bell, 1949); Maastrichtian (McGookey *et al.*, 1972). 59, Upper Edmonton, Canada (Bell, 1949); Maastrichtian. 60, Vermejo, USA (Knowlton, 1917*b*); Maastrichtian (McGookey *et al.*, 1972). 61, Whitemud, Canada (Berry, 1935); Maastrichtian (Bell, 1949). 62, Atanikerdluk, Greenland (based on lists given by Heer (1893) for Atanikerdluk A and B floras); Paleocene (Pedersen, 1976). 63, Fort Union, USA (Brown, 1962); Paleocene. 64, Genesee, Canada (Chandrasekharam, 1974); Paleocene. 65, Menat, France (Laurent, 1912); Paleocene (Russell, in Kedves, 1982). 66, Middle Ravenscrag, Canada (Berry, 1935); Paleocene (Jarzen, 1982*a*). 67, Northwest Greenland (Koch, 1963); Paleocene. 68, Paskapoo, Canada (Bell, 1949); Paleocene. 69, Spitzbergen (Manum, 1962); Paleocene. 70, Upper Ravenscrag, Canada (Berry, 1935); Paleocene (Jarzen, 1982*a*).

Tabulation of data from the floras listed above

	Pteridophytes	Other seed plants	Cycadophytes	Conifers	Angiosperms
Jurassic					
1. Boroldaisky	19	9	9	7	0
2. Borolsaisky	1	2	6	6	0
3. Issyktasky	7	6	5	2	0
4. Karabastausky	10	8	17	17	0
5. Oregon	13	8	26	11	0
6. Oroville	9	2	11	2	0
7. Yorkshire	55	29	60	26	0

Tabulation of data (cont.)

	Pteridophytes	Other seed plants	Cycadophytes	Conifers	Angiosperms
Neocomian–Barremian					
8. Hazelton	9	3	6	2	0
9. Horsetown	6	3	6	7	3
10. Kootenay	9	6	10	4	0
11. Nikanassin	4	3	1	4	0
12. Wealden, Germany	4	1	5	3	0
13. Wealden, Saxony	15	2	7	3	0
14. Wealden, UK	17	2	18	13	0
15. Upper Knoxville	13	3	12	4	0
Aptian–Lower Albian					
16. Almargem	4	1	1	4	0
17. Bullhead	8	4	8	7	0
18. Cercal	7	1	0	4	4
19. Fuson	8	0	1	9	3
20. Kome	48	4	10	17	0
21. Kootenai	16	3	1	4	0
22. Lower Blairmore	15	5	9	10	1
23. Luscar	17	4	10	13	0
24. Potomac, Zone I	33	3	13	20	6
Middle–Upper Albian					
25. Buarcos	11	0	1	6	4
26. Cheyenne	4	0	0	3	11
27. Kingsvale	8	1	1	6	7
28. Nazaré	1	0	0	1	2
29. Pasayten	8	1	2	1	6
30. Potomac, Zone II	9	0	3	12	21
31. Taverede	5	0	0	5	8
32. Upper Blairmore	9	0	1	8	13
Cenomanian					
33. Bingen	2	0	0	6	20
34. Dakota	7	0	3	19	437
35. Dunvegan	10	2	2	8	42
36. Kaltag	6	9	5	17	75
37. Melozi	0	0	0	8	46
38. Nulato	1	0	1	6	8
39. Raritan	8	2	0	11	62
40. Tuscaloosa	9	0	0	14	118
41. Woodbine	0	0	0	2	37

Tabulation of data (cont.)

	Pteridophytes	Other seed plants	Cycadophytes	Conifers	Angiosperms
Turonian–Campanian					
42. Atane	34	5	8	20	97
43. Black Creek	2	0	0	12	58
44. Eutaw	0	0	0	7	37
45. Frontier	8	0	0	0	17
46. Fruitland and Kirtland	4	0	0	0	29
47. Judith River	1	0	0	6	14
48. Magothy	13	3	1	32	208
49. Milk River	6	0	0	6	15
50. Nanaimo	14	1	5	5	62
51. Patoot	21	0	0	15	76
Maastrichtian					
52. Dawson Arkose	5	0	0	0	65
53. Lance	6	1	0	2	54
54. Laramie	14	0	0	3	107
55. Lower Edmonton	1	1	1	5	4
56. Lower Medicine Bow	4	0	0	1	52
57. Raton	7	0	0	0	130
58. St Mary River	2	0	0	2	6
59. Upper Edmonton	1	0	0	1	6
60. Vermejo	14	0	0	7	77
61. Whitemud	1	1	0	2	19
Paleocene					
62. Atanikerdluk	9	1	0	17	143
63. Fort Union	20	1	2	7	120
64. Genesee	3	0	0	4	8
65. Menat	4	0	0	4	38
66. Middle Ravenscrag	2	0	0	11	25
67. Northwest Greenland	2	1	0	1	32
68. Paskapoo	6	1	0	5	23
69. Spitzbergen	6	6	0	14	54
70. Upper Ravenscrag	1	1	0	4	23

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